PROC. BIOL. SOC. WASH.
97(2), 1984, pp. 395–403

ON SMALL BATS OF THE GENUS *PTEROPUS* FROM THE PHILIPPINES

David Klingener and G. Ken Creighton

Abstract.—Analysis of cranial ontogeny in large series of *Pteropus* from the Philippine Islands indicates that bats previously allocated to three different species in the genus are conspecific. The name *Pteropus tablasi* Taylor was based on a very young individual, and the name *Pteropus balutus* Hollister on a very old one. Both are synonyms of *Pteropus pumilus* Miller. *Pteropus pumilus* is a member of the *hypomelanus* species group. *Pteropus tablasi,* when initially described, was mistakenly assigned to the *temmincki* group. *Pteropus pumilus* is distinct from *P. speciosus* and is sympatric with it on at least one island. Some allometric properties of skull growth are described.

In January 1906 Dr. Edgar A. Mearns collected three specimens of *Pteropus* on Miangas (Palmas) and Balut Islands southeast of Mindanao. Miller (1910:394) observed that the two specimens from Miangas resemble *P. speciosus* from the Sulu Archipelago, but are smaller, and based the name *Pteropus pumilus* on them. Andersen (1912:816) examined the paratype of *P. pumilus* and included the species in his *hypomelanus* group. Hollister (1913:111) based the name *Pteropus balutus* on the single specimen from Balut and observed that it approached *P. speciosus* in size, though it resembled *P. pumilus* in coloration of pelage. Taylor (1934:169) described *Pteropus tablasi* on the basis of a single specimen from Tablas Island, east of Mindoro. Taylor assigned *P. tablasi* to Andersen's *temmincki* group. Lawrence (1939:35) referred three specimens from Mindoro to *P. tablasi* and confirmed assignment of the species to the *temmincki* group. Our attempt to identify a small specimen of *Pteropus* from Negros Island in the University of Massachusetts Museum of Zoology (UMA) led to examination of Lawrence's material from Mindoro (Museum of Comparative Zoology, Harvard University, MCZ), the types of *P. pumilus* and *P. balutus* in the National Museum of Natural History (USNM), the type of *P. tablasi* in the American Museum of Natural History (AMNH), and large series of small *Pteropus* from various islands in the Philippine Archipelago housed in the Delaware Museum of Natural History (DMNH). In addition, series of *P. speciosus, P. griseus,* and *P. temmincki capistratus* were also studied.

Taxonomic Discussion

Taxonomic study of megachiropteran bats is complicated by the fact that the skull continues to change in dimensions and shape throughout life. Even when "adult" bats from different localities are compared, ontogenetic factors must be considered when evaluating differences observed. The large number of specimens of small Philippine *Pteropus* now available in collections allows reassessment of the morphological basis of previous taxonomic opinions.

The following measurements were taken by Klingener with dial calipers calibrated to 0.1 mm: greatest length of skull (GLS); diameter of orbit; interorbital

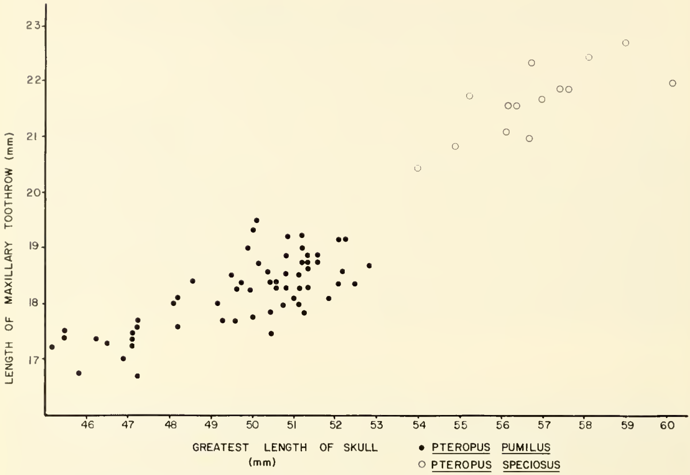

Fig. 1. Regression of maxillary toothrow length (C-M²) on greatest length of skull.

width (IOW); postorbital width (POW); maximum width of braincase (WBC), taken above the squamosal roots of the zygomatic arches; length of maxillary toothrow, measured from the anterior surface of the upper canine tooth to the posterior surface of the second (last) upper molar; and length of molariform toothrow, measured from the anterior surface of the third upper premolar to the posterior surface of the second upper molar, excluding the diminutive second premolar. Few forearm lengths were obtained, as the majority of skins had been prepared in such a way that accurate measurement was impossible. Specimens examined are listed in the Appendix. Many specimens could not be included in the graphs or analyses owing to damage to the skulls during preparation.

In megachiropterans the skull continues to elongate in adults. This elongation may involve backward and dorsal movement of the braincase, as well as elongation of the rostrum in long-faced forms. Lanza (1961) described rostral elongation in *Epomophorus,* and Peterson and Fenton (1970) described changes in the braincase in *Harpyionycteris.* In *Pteropus* both rostral elongation and posterodorsal extension of the braincase occur. As the rostrum lengthens, the small upper second premolar may drop out, and a pronounced diastema appears between the upper canine and the third premolar. Lengthening of the rostrum and expansion of the toothrow produce an increase in maxillary toothrow length as the bat ages (see Felten 1964, fig. 4).

We plotted several dimensions against greatest length of skull. As in the *Harpyionycteris* described by Peterson and Fenton (1970) the postorbital width decreases with age as the braincase extends posteriad, and the ventral deflection of the braincase decreases. The width of the braincase is somewhat variable but

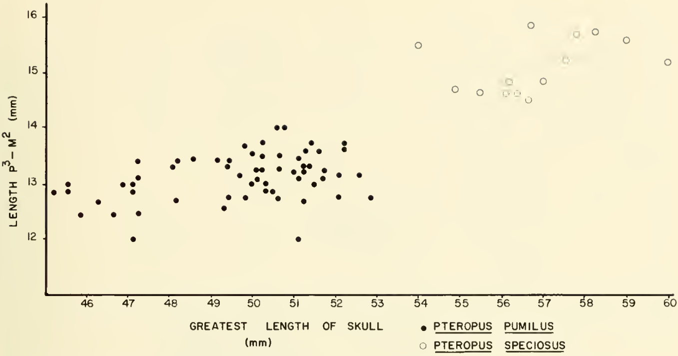

Fig. 2. Regression of molariform toothrow length (P^3-M^2) on greatest length of skull.

remains essentially constant. The maxillary toothrow length clearly increases with skull length (Fig. 1), but a similar increase is not obvious in length of the molariform toothrow (Fig. 2). Increase in the value of the former dimension is due to growth of the rostrum and forward movement of the canines. The skull of the type specimen of *P. tablasi* (AMNH No. 241737) is obviously that of a very young bat. The rostrum is short, the teeth are crowded together, there is no diastema, the cranial sutures are visible, and the braincase shows a pair of weak temporal lines rather than a median sagittal crest. Bats with a skull length of about 50 mm, including the type material of *P. pumilus,* are obviously more mature, with a long rostrum, an obvious diastema, fused sutures, and a variably developed sagittal crest. The older bats agree with the type specimen of *P. tablasi* in coloration of the mantle (yellowish buff) but tend to have darker fur on the body behind the mantle. Numerous specimens are intermediate in size, coloration, and morphology, and the differences are clearly ontogenetic. *Pteropus tablasi* is therefore conspecific with *P. pumilus.*

Pteropus speciosus is easily distinguished from *P. pumilus.* In *P. speciosus* the mantle is dark reddish brown, in contrast to the buffy mantle of *P. pumilus.* Molariform toothrow length in *P. speciosus* ranges from 14.5 to 16 mm; in *P. pumilus* from 12 to 14 mm. Further, bats identified as *P. speciosus* with a skull length of 54 or 55 mm are obviously young bats with short rostra and crowded toothrows. Bats with a skull length approaching 60 mm are obviously more mature. The type specimen of *P. balutus* (USNM No. 144760), with a skull length of 55.4 mm, falls within the size range of *P. speciosus.* The skull, however, is clearly that of a very old bat. The first and second upper molars on both right and left sides have been worn away or have dropped out, and the alveoli have closed over with bone. The upper fourth premolars are worn down to the roots, and the worn third premolars are the only intact molariform teeth in the skull. The mandibular dentition is also worn and lacking some teeth. Coloration of the pelage agrees with *P. pumilus,* and the specimen is certainly a very old individual

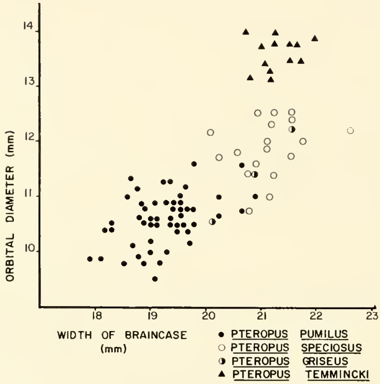

Fig. 3. Regression of orbital diameter on width of braincase.

of that species. (This specimen was not included in Figs. 1 and 2 because the dentition is incomplete.)

Andersen (1912:315, 822), in characterizing the *Pteropus temmincki* species group, stressed the short rostrum and large orbits as distinctive cranial characters. In young bats of other species groups, however, the rostra are short and the orbits large relative to skull length, and some confusion in assignment of bats to the *temmincki* group has resulted. Goodwin (1979:87f) discussed past misidentifications of young specimens of *P. griseus* from Timor as *P. temmincki.* Similarly, Taylor's (1934) assignment of *P. tablasi* to the *temmincki* group was based on his evaluation of the skull of a very young individual. We plotted orbital diameter against braincase width, which is not affected by growth, and found that specimens of *P. temmincki* from the Bismarck Archipelago cluster well above *P. pumilus* (sensu lato, including the type specimen of *P. tablasi*), *P. griseus,* and *P. speciosus* regardless of the age of the bat (Fig. 3). The last three species are all members of Andersen's *hypomelanus* group. *Pteropus pumilus,* then, includes bats previously described as *P. tablasi* and *P. balutus,* and is not a member of Andersen's *temmincki* group.

The known Philippine distribution of *P. speciosus* includes islands of the Sulu Archipelago and a small area of the Zamboanga Peninsula of Mindanao. Sanborn (1952:99) reported on two specimens in the Field Museum of Natural History, one from Dumaguete, Negros Island, and the other from Mactan Island near Cebu. We examined the former specimen, and Dr. Karl F. Koopman (pers. comm.) examined the latter. Both are young specimens of a larger species of *Pteropus,* probably *P. hypomelanus. P. speciosus* and *P. pumilus* are sympatric at least on Sanga-Sanga Island in the Sulu Archipelago.

Basic descriptive statistics for cranial measurements of specimens examined in this study are presented in Table 1. The "diastema" ("DIAS") was calculated by subtracting molariform toothrow length from maxillary toothrow length; increase in its value is an indication of rostral elongation. *Pteropus pumilus* and *P. speciosus* are apparently sexually dimorphic in size (males being slightly larger) and *P. pumilus* from different islands exhibit significant geographic variation in several cranial measurements. Two-way analyses of variance (by sex and locality) were computed for all cranial measurements of adult *P. pumilus. Pteropus pumilus* are significantly sexually dimorphic ($P < 0.005$) in GLS, maxillary toothrow length, and "diastema" length. Too few specimens of female *P. speciosus* were available to calculate a two-way analysis of variance by sex and locality; however, samples of male *P. speciosus* from four islands did not differ significantly (one-way ANOVA; $P > 0.1$). These samples were pooled and the composite sample ($n = 8$) was compared with adult female *speciosus* from Malanipa Island ($n = 6$). One-way ANOVA revealed significant sexual dimorphism in *P. speciosus* ($P < 0.05$) in GLS, maxillary toothrow length, "diastema" length, WBC, and POW. In both *P. pumilus* and *P. speciosus* males average slightly larger than females in all cranial measurements. Among the features evaluated, both species are most dimorphic in "diastema" length. A sample of twelve *P. temmincki* (4 males, 8 females) from New Britain was not significantly dimorphic in any of the cranial features measured, though males average larger for most traits (Table 1).

Secondary sexual dimorphism is marked in epomophorine pteropodids, the males being larger. Lanza (1961) documented almost complete nonoverlap of males and females in some cranial dimensions in *Epomophorus*. Our findings on *Pteropus* do not necessarily indicate true secondary sexual dimorphism, however. Larger bats with longer skulls and rostra tend to be male. That situation could be an effect of higher earlier mortality of females, possibly owing to stresses of pregnancy and lactation, or an effect of an intrinsic morphological difference between the sexes. Without an independent method of ageing our specimens, we cannot eliminate either alternative.

After accounting for sexual dimorphism, *P. pumilus* exhibit significant geographic variation in GLS, maxillary toothrow length, molariform toothrow length, "diastema" length, and POW ($P < 0.025$). Although specimens that were obviously immature were excluded from the statistical analyses, it seems likely that differences in age composition of local samples may account for much of the variation among the populations of *P. pumilus* studied. Coloration of pelage in *P. pumilus* is variable. The buffy mantle varies little with age or locality. The fur of the rest of the body, both dorsally and ventrally, varies in shade considerably within samples, although very young bats tend to be lighter. Individual adult bats from the Sulu Archipelago can be matched with individual adults from Mindoro and Negros Islands. Bats from Camiguin, however, differ in color pattern from all other populations in the species, having steel-gray fur on the head, shoulders in front of the mantle, and anterior part of the chest. This pattern is found in Camiguin specimens of all ages and is not seen in specimens from any other island. At present we do not choose to recognize the Camiguin population as a separate taxonomic entity.

We investigated the intraspecific scaling (size allometry) of three dimensions with cranial length for each species using least-squares regression (Ricker 1973) on log-transformed data. The allometric relationships among dimensions for each species are given by coefficients (slopes) of the regressions presented in Table 2.

Patterns of size allometry differ somewhat among the three species. All species

Table 1.—Cranial measurements of small *Pteropus*.†

Sex	(N)	GLS	Orb. Dia.	C–M^2	P^3–M^1	WBC	POW	'Diastema'
				Pteropus pumilus, type series, Palmas Island				
M	1	†51.3	11.2	18.8	12.7	19.3	8.0	6.1
F	1	—	10.5	17.8	12.8	—	—	5.0
				Pteropus tablasi, holotype, Tablas Island				
?	1	†45.2	9.8	17.2	12.9	18.6	9.0	4.3
				Pteropus balutus, holotype, Balut				
F	1	†55.4	11.6	—	—	20.7	6.8	—
				Pteropus pumilus, Mindoro				
M	1	†52.1	10.7	19.1	13.2	20.2	7.6	5.9
F	1	48.2	10.9	18.1	13.4	19.3	7.9	4.7
				Pteropus pumilus, Batu Batu				
M		†49.56 ± 1.91 (45.5–51.4) 7	10.65 ± .21 (10.4–10.9) 6	18.69 ± .71 (17.5–19.5) 7	13.51 ± .33 (13.0–14.0) 7	19.34 ± .79 (18.2–20.6) 7	8.00 ± .88 (7.1–9.4) 6	5.17 ± .63 (4.5–6.2) 7
F		48.71 ± 2.32 (45.9–51.7) 7	10.20 ± .66 (9.5–11.0) 5	17.76 ± .80 (16.7–18.8) 8	13.04 ± .63 (12.0–13.8) 8	18.81 ± .41 (18.1–19.4) 7	8.05 ± .79 (6.6–8.8) 6	4.72 ± .56 (4.1–5.6) 8
				Pteropus pumilus, Sanga Sanga				
M		†50.85 ± .88 (49.5–52.7) 18	10.79 ± .37 (9.9–11.6) 18	18.45 ± .44 (17.7–19.2) 19	13.31 ± .31 (12.8–14.0) 19	19.36 ± .62 (17.9–20.9) 19	7.83 ± .76 (6.4–9.1) 18	5.14 ± .31 (4.5–5.6) 19
F		50.6 ± 1.50 (48.2–52.2) 7	10.84 ± .05 (10.8–10.9) 5	18.12 ± .79 (16.5–19.1) 9	13.37 ± .33 (12.7–13.7) 9	19.14 ± .47 (18.4–19.6) 8	7.64 ± .87 (6.3–8.7) 7	4.75 ± .62 (3.5–5.5) 9
				Pteropus pumilus, Camiguin				
M		†49.73 ± 3.25 (46.4–52.9) 3	10.33 ± .31 (10.0–10.6) 3	18.50 ± .28 (18.3–18.7) 2	12.80 ± .14 (12.7–12.9) 2	19.40 ± .40 (19.0–19.8) 3	8.80 ± .61 (8.4–9.5) 3	5.70 ± .14 (5.6–5.8) 2
F	3	49.93 ± 1.01 (49.3–51.1)	10.43 ± .21 (10.2–10.6)	18.03 ± .35 (17.7–18.4)	12.46 ± .42 (12.0–12.8)	18.97 ± .15 (18.8–19.1)	7.37 ± .72 (6.9–8.2)	5.57 ± .45 (5.1–6.0)

Table 1.—Continued.

Sex	(N)	GLS	Orb. Dia.	$C-M^2$	P^3-M^2	WBC	POW	'Diastema'
				Pteropus pumilus, Negros				
M		†49.23 ± 2.23 (45.5–51.5) 7	10.49 ± .51 (9.8–11.1) 9	18.14 ± .73 (17.0–19.0) 9	13.01 ± .20 (12.7–13.4) 9	19.23 ± .60 (18.3–20.3) 9	8.58 ± .78 (7.4–9.8) 9	5.13 ± .62 (4.3–5.8) 9
F	7	47.64 ± 1.63 (46.3–51.1) 7	10.47 ± .26 (10.1–10.9) 7	17.54 ± .46 (17.0–18.3) 7	12.94 ± .27 (12.5–13.3) 7	19.16 ± .30 (18.7–19.5) 7	9.16 ± .52 (8.5–9.9) 7	4.60 ± .38 (4.0–5.2) 7
				Pteropus speciosus, Malanipa Island				
M	3	†57.1 ± 2.70 (54.0–59.0)	11.73 ± .86 (10.8–12.5)	21.93 ± 1.16 (20.6–22.7)	15.60 ± .20 (15.4–15.8)	21.00 ± .36 (20.6–21.3)	8.07 ± .57 (7.6–8.7)	6.33 ± 1.0 (5.2–7.1)
F	6	56.85 ± .67 (56.2–57.8)	11.70 ± .51 (11.0–12.5)	21.57 ± .66 (20.6–22.5)	15.17 ± .56 (14.5–15.9)	20.83 ± .30 (20.3–21.1)	7.43 ± .36 (7.0–7.9)	6.40 ± .30 (5.9–6.7)
				Pteropus speciosus, Mindanao, Zamboanga Peninsula				
M	1	†60.3	12.4	22.0	15.2	21.6	7.2	6.8
				Pteropus speciosus, Sanga Sanga				
M		†60.13 ± 3.05 (56.8–62.8) 3	12.2 1	22.63 ± .98 (21.5–23.2) 3	15.46 ± .85 (14.5–16.1) 3	22.00 ± .85 (21.4–22.6) 3	8.10 ± 1.13 (8.3–8.7) 3	7.17 ± .21 (7.0–7.4) 3
				Pteropus speciosus, Sibutu				
M	2	†59.75 (58.6–60.9)	12.15 (11.8–12.5)	22.85 (22.5–23.2)	16.10 (16.0–16.2)	21.55 (21.5–21.6)	8.10 (7.9–8.3)	6.75 (6.5–7.0)
				Pteropus temmincki, New Britain				
M	4	†57.05 ± 1.13 (55.5–58.0)	13.75 ± .17 (13.5–13.9)	20.90 ± .77 (20.0–21.8)	14.43 ± .17 (14.2–14.6)	21.42 ± .50 (20.8–22.0)	9.55 ± .78 (9.0–10.7)	6.48 ± .85 (5.6–7.6)
F		56.86 ± .79 (56.1–58.1) 7	13.62 ± .29 (13.2–14.0) 8	20.94 ± .70 (19.7–21.9) 7	14.93 ± .40 (14.3–15.4) 7	21.23 ± .38 (20.8–21.8) 7	8.77 ± 1.10 (7.5–10.6) 7	6.01 ± .64 (5.2–7.0) 7

† Table 1: Measurements (mm; $\bar{x}$ ± SD; range; sample size) of specimens of *Pteropus* examined.

Table 2.—Intraspecific scaling of cranial measurements.

Taxon	N	Dependent variable (log e)	Independent variable (log e)	R^2	Coefficient (slope)	$P\leq$*
P. pumilus	61	P^3–M^2	GLS	.16	.32	.0001
P. speciosus	20	P^3–M^2	GLS	.40	.64	NS
P. temmincki	13	P^3–M^2	GLS	.00016	.02	NS
P. pumilus	60	C–M^2	GLS	.61	.70	.001
P. speciosus	20	C–M^2	GLS	.70	.95	NS
P. temmincki	13	C–M^2	GLS	.55	1.55	NS
P. pumilus	60	"DIAS"	GLS	.42	1.64	.014
P. speciosus	20	"DIAS"	GLS	.58	1.71	.053
P. temmincki	13	"DIAS"	GLS	.63	5.05	.005

* Two-tailed 'T' test of H_0: observed slope = isometric slope = 1.0.

show positive allometry of "diastema" length with cranial length. Within each species, larger bats have absolutely and relatively longer "diastemata." To the extent that size allometry within species reflects the patterns of growth allometry it appears that rostral elongation occurs throughout life in these bats by elongation of the "diastema." In *P. temmincki,* though the rostrum is always short, relative growth in the rostral region anterior to the molariform teeth is pronounced. Length of the maxillary toothrow increases isometrically with cranial length in *P. speciosus,* with strong positive allometry in *P. temmincki,* and with negative allometry in *P. pumilus,* reflecting the pattern of relative scaling found for "diastema" length vs. GLS. Molariform toothrow length shows the lowest correlation with cranial length and the flattest slope of the three regressions for each species. In these pteropodids this dimension increases only minimally with increasing cranial length, and it also shows much less variation with age and sex within a species than the other measurements.

Our object in presenting this analysis of size allometry is to emphasize the need to account for continuous ontogenetic change when doing species level taxonomy of pteropodids. Exceptionally old individuals of one species may overlap in cranial measurements with young individuals of another. Very young specimens that appeared distinctive to the original describer are considerably less so when larger series are available for comparison. We found simple bivariate plots of cranial measurements to be adequate and effective for displaying the absolute and relative differences in cranial proportions among the species surveyed and the range of variation to be expected within each species.

Acknowledgments

We thank the following persons for permission to study specimens in their care: Dr. Karl F. Koopman, American Museum of Natural History; Dr. Michael D. Carleton, National Museum of Natural History; Ms. Maria E. Rutzmoser, Museum of Comparative Zoology; Dr. David Niles, Delaware Museum of Natural History; and Dr. Patricia W. Freeman, then of the Field Museum of Natural History. We also thank Drs. Koopman, Lawrence R. Heaney, and Richard W. Thorington, Jr. for assistance during the project. We are deeply indebted to Dioscoro S. Rabor, whose field work in the Philippines produced many of the specimens upon which this report is based. Creighton performed the statistical analyses on the Michigan Terminal System using programs maintained by the Statistical Research Laboratory of the University of Michigan. Publication costs were partly defrayed by the Crampton Research Fund, University of Massachusetts.

Literature Cited

Andersen, K. 1912. Catalogue of the Chiroptera in the collection of the British Museum. Second Edition. Vol. I: Megachiroptera.—British Museum (Natural History), London. ci + 854 pp.

Felten, H. 1964. Flughunde der Gattung *Pteropus* von Neukaledonien und den Loyalty-Inseln (Mammalia, Chiroptera).—Senckenbergiana Biologica 45(6):671–683.

Goodwin, R. E. 1979. The bats of Timor: systematics and ecology.—Bulletin of the American Museum of Natural History 163(2):73–122.

Hollister, N. 1913. Two new Philippine fruit bats.—Proceedings of the Biological Society of Washington 26:111–112.

Lanza, B. 1961. Alcune particolarità delle pliche palatine e dell'accrescimento postembrionale del cranio in *Epomophorus* (Mamm.; Megachiroptera).—Monitore Zoologico Italiano 68(3–4):170–184.

Lawrence, B. 1939. Mammals. *In* Barbour, T., B. Lawrence, and J. L. Peters. Collections from the Philippine Islands.—Bulletin of the Museum of Comparative Zoology 86(2):25–128. Pp. 28–73.

Miller, G. S., Jr. 1910. Descriptions of two new genera and sixteen new species of mammals from the Philippine Islands—Proceedings of the United States National Museum 38(1757):391–404, pls. 18–20.

Peterson, R. L., and M. B. Fenton. 1970. Variation in the bats of the Genus *Harpyionycteris*, with the description of a new race.—Life Sciences Occasional Papers Royal Ontario Museum 17: 1–15.

Ricker, W. E. 1973. Linear regressions in fishery research.—Journal of the Fisheries Research Board of Canada 30(3):409–434.

Sanborn, C. C. 1952. Philippine zoological expedition 1946–1947—Mammals.—Fieldiana: Zoology 33(2):89–158.

Taylor, E. H. 1934. Philippine land mammals.—Monographs of the Bureau of Science, Manila 30: 1–548.

(DK) Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003; (GKK) Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109.

Appendix

List of Specimens Examined

Pteropus pumilus (93).—Palmas (Miangas) Island, 2 (USNM); Balut Island, 1 (USNM); Bongao Island, 4 (DMNH); Batu-Batu Island, 12 (DMNH); Sanga-Sanga Island, 30 (DMNH); Camiguin Island, 22 (DMNH); Negros Island, 1 (UMA), 17 (DMNH); Mindoro Island, 3 (MCZ); Tablas Island, 1 (AMNH).

Pteropus speciosus (21).—Mindanao, Zamboanga, 1 (AMNH); Malanipa Island, 10 (AMNH), 4 (USNM); Sanga-Sanga Island, 4 (DMNH); Sibutu Island, 2 (DMNH).

Pteropus griseus (3).—Timor, 3 (AMNH).

Pteropus temmincki capistratus (14).—New Britain, 12 (AMNH), 2 (USNM).